PHYLOGENETIC RELATIONSHIPS OF THE *CORALLIOZETUS* CLADE OF CHAENOPSID BLENNIES, WITH DESCRIPTION OF A NEW GENUS (TELEOSTEI, BLENNIOIDEI)

Philip A. Hastings

ABSTRACT

A parsimony analysis of 53 morphological characters was used to hypothesize the relationships of the species of the chaenopsid genera *Coralliozetus* and *Protemblemaria*. A single most parsimonious topology was obtained (Fig. 1), with the following implications. Species currently allocated to these genera, together with the genus *Emblemariopsis*, form a monophyletic group (termed the *Coralliozetus* clade) whose sister group is the *Chaenopsis* clade (sensu Hastings and Springer, 1994). The genus *Coralliozetus* is monophyletic and distinctive, with the six included species sharing more than twenty apomorphies. As currently construed, the genus *Protemblemaria* is not monophyletic. *Protemblemaria lucasana* Stephens, 1963 is either the sister group of *Emblemariopsis* (in the shortest topology), or of *Coralliozetus* plus the other two species of *Protemblemaria* (in a topology one step longer than the most parsimonious). A new generic name (*Cirriemblemaria*) is provided for this species to achieve a monophyletic classification. A synapomorphy for the genus *Emblemariopsis* is proposed, and *Coralliozetus tayrona* Acero, 1987 is included in *Emblemariopsis*. The *Coralliozetus* clade includes two transisthmian species pairs.

The Chaenopsidae includes about 80 species of small (less than 150 mm SL) blennioid fishes typically associated with rock or coral reefs or adjacent rubble areas (Stephens, 1963; Hastings and Springer, 1994). The common name, tube blennies, comes from their propensity for occupying vacant invertebrate tests. This family was recently expanded, and the traditional members (sensu Stephens, 1963) were restricted to the subfamily Chaenopsinae (Hastings and Springer, 1994).

Included within the Chaenopsinae are three apparently monophyletic groups (Hastings and Springer, 1994), the *Acanthemblemaria* clade (intrarelationships hypothesized by Hastings, 1990 and Almany and Baldwin, 1996), the *Chaenopsis* clade (intrarelationships hypothesized by Hastings, 1992a) and the *Coralliozetus* clade. The latter clade includes the genera *Coralliozetus*, erected by Evermann and Marsh in 1900 for a new species (*C. cardonae*) from Puerto Rico, *Protemblemaria*, erected by Stephens in 1963 for *Emblemaria bicirris* Hildebrand, 1946 from the eastern Pacific and a new species (*P. lucasana*) from the Gulf of California, and *Emblemariopsis* erected by Longley in 1927 for a new species (*E. diaphana*) from Florida. These three nominal genera were recently hypothesized to be closely related and consequently all were synonymized under *Coralliozetus* by Acero (1984a, 1987). Hastings and Springer (1994) also hypothesized a close relationship of these genera, but did not discuss the nomenclatural implications of this finding and did not hypothesize relationships within this clade.

This paper presents a hypothesis of relationships within the *Coralliozetus* clade, including relationships of the species of *Coralliozetus* (sensu Stephens, et al., 1966) and *Protemblemaria* (sensu Stephens, 1963, 1970), based on a parsimony analysis of morphological characters. Implications of this phylogenetic hypothesis for the nomenclature

of these fishes and for the biogeography of the Caribbean and eastern Pacific are discussed.

MATERIALS AND METHODS

The phylogenetic analysis is based on both external and internal characters, but concentrates on osteology. Osteological specimens were double stained for bone and cartilage according to Dingerkus and Uhler (1977).

Each of the six species of *Coralliozetus* and the three nominal species of *Protemblemaria* were scored as separate taxa in the phylogenetic analysis (Table 1). One of these, *Protemblemaria lucasana* Stephens, 1963, is placed in a new genus, *Cirriemblemaria*, based on the results of this phylogenetic analysis (see below) and referred to under that genus throughout this paper. The recently described *Coralliozetus tayrona* Acero, 1987 and three species of *Emblemariopsis* (see Material Examined) were examined, but these were included under a single terminal taxon (*Emblemariopsis*) in the phylogenetic analysis because they shared identical states for all included characters, and shared a hypothesized apomorphy (see Results).

Representatives of all other chaenopsid genera were examined, but were scored under five terminal taxa based on recently published phylogenetic hypotheses. The "*Chaenopsis* clade" includes *Chaenopsis, Lucayablennius, Hemiemblemaria, Emblemaria* and *Tanyemblemaria* (Hastings, 1992a). The "*Acanthemblemaria* clade" includes *Acanthemblemaria* and *Ekemblemaria* (Hastings, 1990, 1992b). These two clades, together with the *Coralliozetus* clade, constitute a monophyletic Chaenopsinae based on seven hypothesized synapomorphies (Hastings and Springer, 1994). *Stathmonotus, Mccoskerichthys*, and *Neoclinus* are hypothesized to be, respectively, the first, second, and third sister groups of the Chaenopsinae (Fig. 1) based on, respectively, 6, 8, and 8 synapomorphies (Hastings and Springer, 1994). These previously hypothesized relationships were incorporated into the phylogenetic analysis by including three "out group" characters (Table 1). Character 54, uniting the members of the Chaenopsinae (node 4, Fig. 1), was assigned a weight of 7, character 55, uniting *Stathmonotus* with the Chaenopsinae (node 3), was assigned a weight of 6, and character 56, uniting *Mccoskerichthys* with *Stathmonotus* and the Chaenopsinae (node 2), was assigned a weight of 8. All other characters (1-53) received a weight of 1.

Characters and character states used in the phylogenetic analysis are discussed in the Results section, and character scores for all terminal taxa are given in Table 1. While no characters were polymorphic within the included species, some were polymorphic for those terminal taxa including more than one species. For those terminal taxa, states for polymorphic characters were scored in either of two ways. For those clades with recently hypothesized species-level phylogenies, the terminal taxon was scored as the hypothesized ancestral state for that clade, but where the ancestral condition was equivocal, the terminal taxon was scored as polymorphic. Multistate characters were considered unordered except for character 24; its ordering scheme is discussed in the Results section. Where it could be unequivocally determined, the plesiomorphic condition for the Chaenopsinae (node 4, Fig. 1) was assigned state 0 except for characters 2, 13, 17, 30, and 31 that follow the coding scheme of Hastings and Springer (1994). Sexually dimorphic characters included in the phylogenetic analysis were coded only for the sex that differed from outgroups (females in all characters except 36). The condition in the opposite sex is indicated parenthetically at the end of each character description.

Parsimony analyses were conducted with the branch-and-bound algorithm of PAUP (Swofford, 1991), and trees were rooted at *Neoclinus* (Hastings and Springer, 1994). Character evolution was evaluated using MacClade (Maddison and Maddison, 1992).

MATERIAL EXAMINED. —All material examined for the genera *Coralliozetus, Protemblemaria, Cirriemblemaria*, and *Emblemariopsis* are listed below. Material examined for other taxa are listed in Hastings (1990, 1992a, 1992b) and Hastings and Springer (1994). Collection abbreviations

Table 1. Character scores for taxa used in the phylogenetic analysis. Polymorphic characters are as follows: a = states 0 and 1; b = states 1 and 2; c = states 0 and 2. Characters 54, 55, and 56 are "outgroup characters" (see text).

	Character number				
	1-10	11-20	21-30	31-40	41-50	51-56
Coralliozetus springeri	1000111100	0011110111	1111111112	0111111111	0000000001	110111
Coralliozetus cardonae	1000111100	0011110111	1111111111	0111111111	0000000001	111111
Coralliozetus angelicus	1000111100	0011110111	1111111112	0111111000	0000000000	111111
Coralliozetus rosenblatti	1000111100	4011110111	1111111112	0111100002	1111000000	111111
Coralliozetus boehlkei	1000111100	0011110111	1112111112	0111100000	1111111100	110111
Coralliozetus micropes	1000111100	0011110111	1112111112	0111100000	1111111100	111111
Protemblemaria bicirris	1000111111	1100001000	0000000001	1001000000	0000000011	100111
Protemblemaria punctata	1000111111	1100001000	0000000001	1000000001	0000000011	110111
Cirriemblemaria lucasana	1011000002	3010001000	0000000001	0110100000	0000000011	100111
Emblemariopsis	1011000000	0010001000	000000a011	1a10100000	000000000c	010111
Chaenopsis clade	110a000000	0a10001000	00000aa0a1	aa0a0a0000	000000000c	aaa111
Acanthemblemaria clade	0100000000	b010001000	0000000001	1000000000	00000000a0	01a111
Stathmonotus	010010a000	4012001000	00?0001010	1101000000	000000000c	101110
Mccoskerichthys	0100001100	3000001000	0000001000	0000000000	0000000003	000100
Neoclinus	0100021100	c000000000	0000011000	0000010000	0000000013	000000

follow Leviton et. al. (1985). The number of specimens in each lot, as well as the number of cleared and stained (CS) specimens, are indicated parenthetically.

Coralliozetus angelicus: SIO 59-210 (136), SIO 61-225 (228), SIO 61-232 (113), SIO 65-341 (79), UAZ 77-20-1 (144, 40 CS), UAZ 77-25-1 (5), UAZ 77-42-1 (16, 2 CS*). C. boehlkei*: UAZ 69-46-15 (6), UAZ 69-48-7 (74, 2 CS), UAZ 73-60-1 (3), UAZ 77-25-2 (8), UAZ 77-41-9 (99, 2 CS). *C. cardonae*: ANSP 113946 (65), ANSP 144996 (25, 2 CS), ANSP 115020 (93), UF 10748 (1), UMML 12902 (38). *C. micropes*: CAS 58524 (138), SIO 61-274 (142), SIO 65-331 (50), UAZ 71-36-3 (30, 2 CS), UAZ 74-34-13 (121), UAZ 74-36-21 (69), UAZ 74-37-23 (54), UAZ 84-17-1 (3, 1 CS). *C. rosenblatti*: LACM 32086 (18), SIO 61-225 (53), SIO 61-248 (55), SIO 61-256 (48, 2 CS), UAZ 72-106-3 (4), UAZ 85-8-1 (6, 2 CS), UAZ 95-2-1 (11). *C. springeri*: SIO 67-34 (53, 2 CS), SIO 67-37 (20), UAZ 68-74-15 (3), UAZ 85- 14-2 (4), UAZ 85-15-3 (2), UAZ 85-17-2 (8, 2 CS). *Protemblemaria bicirris*: SIO 62-726 (90), UAZ 66-23-6 (7), UAZ 71-61-7 (44), UAZ 77-66-3 (11), UAZ 71-67-2 (8), UAZ 73-94-2 (7, 2 CS), UAZ 73-119-3 (17, 2 CS), UAZ 74-48-4 (22, 7 CS), UAZ 74-87-9 (22), UAZ 95-3-1 (2 CS). *Cirriemblemaria lucasana*: SIO 65-32 (9), SIO 65-317 (23), SIO 65-329 (19), SIO 65-343 (44), SIO 65-347 (8, 2 CS), UAZ 70-23-9 (2), UAZ 72-87-3 (5), UAZ 73-94-3 (14, 2 CS). *P. punctata*: ANSP 103562 (18), ANSP 103564 (13), ANSP 103565 (18, 2 CS), ANSP 103567 (9). *Emblemariopsis diaphana*: UF 16193 (4 radiographs), UF 11882 (5, 1 CS, 4 radiographs), UF 47329 (1), UMML 9230 (7). *E. leptocirris*: UF 12462 (2 radiographs). *E. signifera*: FMNH 87930 (5), FMNH 94007 (1 radiograph), FMNH 96852 (4), UF 18902 (1 CS), UMML 12234 (1 radiograph), USNM 83144 (1 radiograph), USNM 119877 (1 radiograph). *E. tayrona*: UMML 34185 (4, 1 CS).

RESULTS

MONOPHYLY OF *EMBLEMARIOPSIS* SENSU STEPHENS, 1970.

A unique character state was observed in the species of *Emblemariopsis* examined in this study. In these three species, the distal portion of the neural spine of the penultimate vertebra is truncate and the single epural is expanded proximally occupying the position
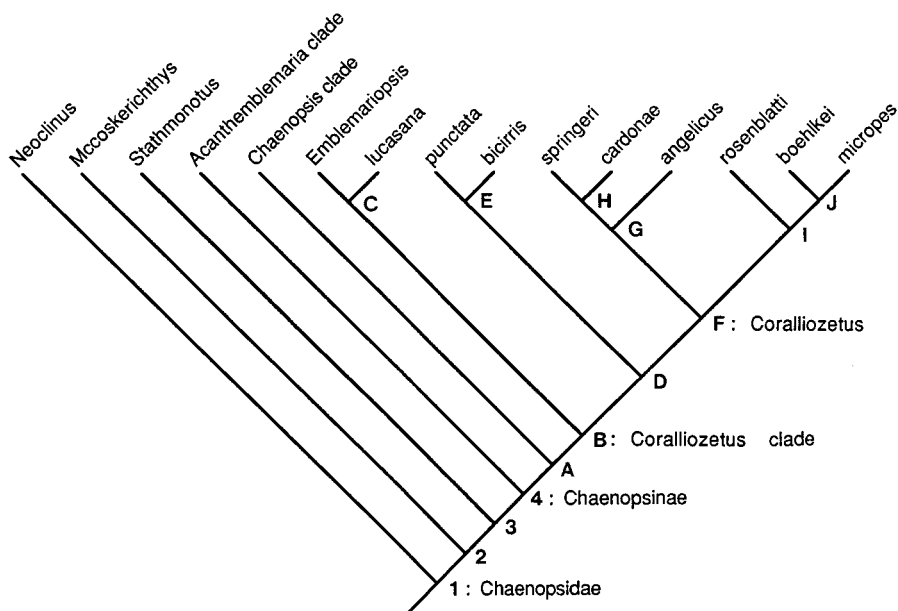
Figure 1. Hypothesized phylogenetic relationships of the *Coralliozetus* clade (single most parsimonious topology, CI = 0.71). Character support for nodes A through J are discussed in the text, while outgroup relationships (nodes 1-4) reflect the hypotheses of Hastings and Springer (1994).

of the neural spine (Fig. 2A). A truncate penultimate neural spine is also present in the recently described *Coralliozetus tayrona* Acero, 1987, but not in any other species examined. In other chaenopsids, the neural spine of the penultimate vertebra is long, thin, and similar to that of more anterior vertebrae (Fig. 2B).

PARSIMONY ANALYSIS

A single most parsimonious topology, requiring 118 steps (excluding the three outgroup characters; CI = 0.71) was found (Fig. 1). Characters supporting this topology are discussed below, followed by a discussion of character support for selected alternative topologies.

Node A. - The species of *Coralliozetus* and *Protemblemaria*, together with *Emblemariopsis* and the *Chaenopsis* clade are hypothesized to form a monophyletic group (Fig. 1) based on a single synapomorphy.

Character 1. In all species above node A, the epural is free in that it does not insert into a bony sheath on the dorsal surface of the urocentral vertebra (state 1; Fig. 2A, B). In other chaenopsins (i.e., *Ekemblemaria* and most species of *Acanthemblemaria*), as well as outgroups of the Chaenopsinae (*Neoclinus, Mccoskerichthys*, and *Stathmonotus*), the epural slips into a bony sheath on the dorsal side of the urocentral vertebra (state 0; character 30 in Hastings and Springer, 1994). A few species of *Acanthemblemaria* also lack this sheath, but these species are well-nested within a recently hypothesized phylogeny of *Acanthemblemaria* species (Hastings, 1990), and absence of the sheath appears to be derived independently at node A and within *Acanthemblemaria*.
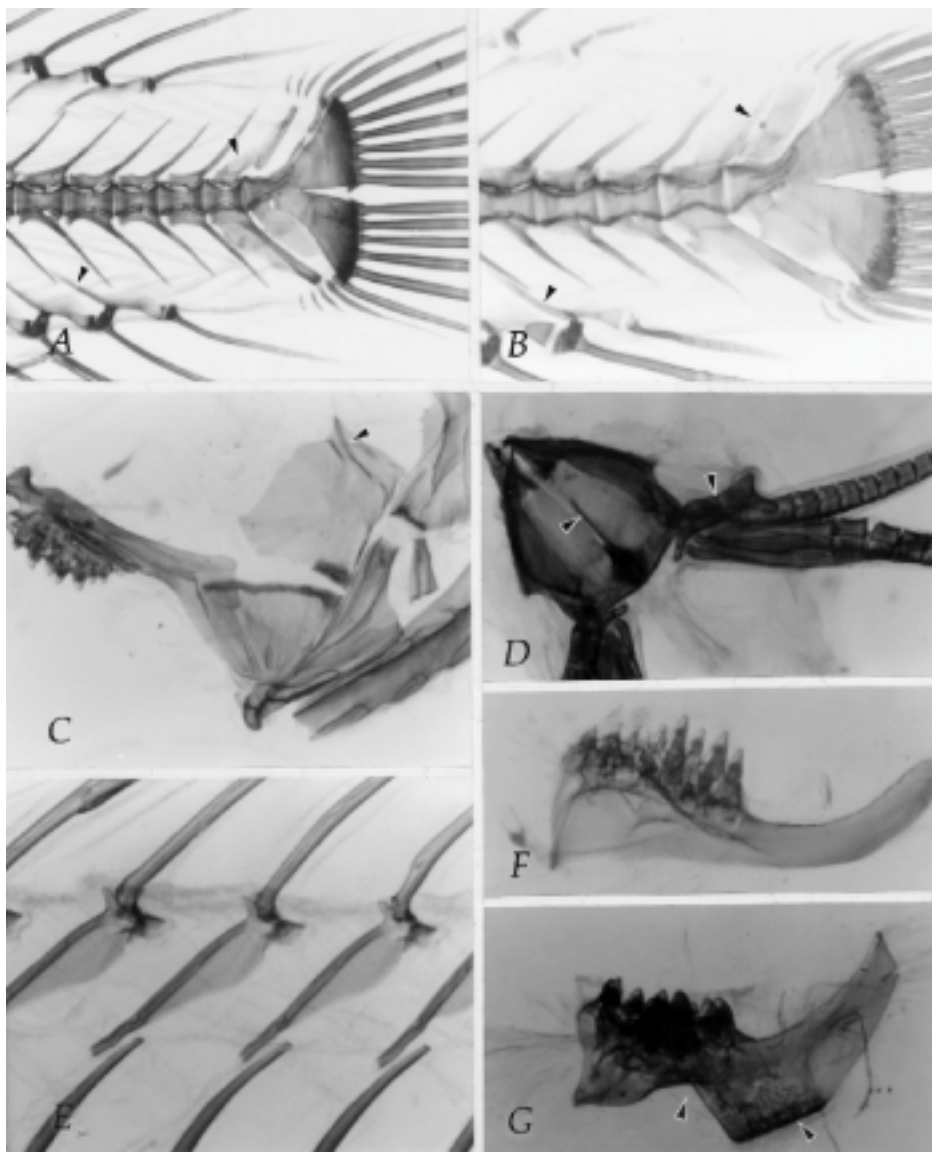
Figure 2. Osteology of selected cleared-and-stained chaenopsids illustrating hypothesized synapomorphies. A) Caudal fin of *Emblemariopsis diaphana* (UF 11882); upper arrow indicates the truncated neural spine of the penultimate vertebra, a hypothesized synapomorphy of the genus *Emblemariopsis*; lower arrow indicates the posteriormost anal-fin proximal radial which lies just posterior to a hemal spine (character 19, state 0). B) Caudal fin of *Coralliozetus angelicus* (UAZ 77-42-1); upper arrow indicates the well-developed neural spine of the penultimate vertebra; lower arrow indicates the posteriormost anal-fin proximal radial, which lies just anterior to a hemal spine (19, 1). C) Left suspensorium of *Coralliozetus angelicus* (UAZ 77-42-1); arrow indicates the lateral projection of the metapterygoid (6, 1). Note also the short row of palatine teeth (23, 1) , and the absence of a mesopterygoid (35, 1). D) Pelvis and pelvic fin of *Coralliozetus micropes* (UAZ 84-17-1); arrow to left indicates the anterior process (8,1); arrow to right indicates the reduced pelvic-fin spine (21, 1). Note also the relatively short and wide pelvis (22, 1). E) Lateral view of "closed" proximal radials supporting spines (18, 1) in the dorsal fin of *Coralliozetus boehlkei* (UAZ 69-48-7). F) Medial view of ceratobranchial 5 of *Protemblemaria bicirris* (UAZ 95-3-1). G) Medial view of ceratobranchial 5 of *Coralliozetus micropes* (UAZ 84-17-1). Left arrow in G) indicates the interrupted ventral flange (45, 1), which in continuous (45, 0) in F). Right arrow in G) indicates the thickened ventral margin of the ventral flange (46, 1), which is thin (46, 0) in F). Note also in G) the relatively acute angle formed by the ventral margin of the posterior flange (42, 1), compared to the more gently upward curve (42, 0) in F).

Node B. - The six species of *Coralliozetus*, the three species previously allocated to *Protemblemaria*, and the genus *Emblemariopsis* are hypothesized to form a monophyletic group (Fig. 1) termed the *Coralliozetus* clade by Hastings and Springer (1994). This is supported by a single synapomorphy.

Character 2. Posterior to the orbital region, blennioids possess a ridge on the lateral side of the sphenotic above the insertion of the hyomandibular that is contiguous anteriorly with a similar ridge on the frontal. In most blennioids, this ridge lacks a spine (state 0), but in most chaenopsids, this ridge bears a lateral process called the sphenotic spine (state 1; character 7 in Hastings and Springer, 1994). However, in all species above node B, this spine is absent (state 0), a condition that appears to represent a loss of the sphenotic spine within the Chaenopsidae.

Node C. - In the most parsimonious topology (Fig. 1), the genus *Protemblemaria* sensu Stephens, 1963, 1970 is not monophyletic. *Cirriemblemaria lucasana* is hypothesized to be the sister group of *Emblemariopsis* based on two synapomorphies.

Character 3. In mature males of *C. lucasana* and the species of *Emblemariopsis* examined in this study, the testicular tissue is located relatively far anteriorly and, as a consequence, the vas deferens is relatively long (state 1). In mature males of other chaenopsids, testicular tissue extends from the anterior abdominal cavity posteriorly to the region of the vent, and the vas deferens is relatively short (state 0).

Character 4. In *C. lucasana* and *Emblemariopsis*, the dorsal surface of the nasal bone bears an ossified ridge that is evident externally (state 1). In most other chaenopsids, the nasals are rounded to flattened dorsally and lack ridges on their dorsal surface (state 0), with the exception of *Emblemaria* and *Tanyemblemaria* which have nasal ridges (Hastings, 1992a).

Node D. - *Protemblemaria bicirris, P. punctata* and the six species of *Coralliozetus* are hypothesized to form a monophyletic group (Fig. 1) based on four synapomorphies.

Character 5. In these species, the dorsal edge and the vertical plate of the urohyal are reduced resulting in a crescent-shaped or slightly "L-shaped" (sensu Kusaka, 1974) urohyal in lateral view (state 1). In most chaenopsids, the dorsal edge and vertical plate of the urohyal are larger and the urohyal is more triangular in lateral view (state 0). The exception is *Stathmonotus* which has a crescent-shaped urohyal, but this genus is not closely related to the species above node D (Hastings and Springer, 1994).

Character 6. In all species above node D, the dorsal portion of the metapterygoid has a prominent lateral projection (state 1; Fig. 2C); this projection is evident as a crease or sharp angle between the dorsal and ventral portions of the metapterygoid, and accommodates the insertion of a portion of the cheek musculature on the dorsomedial surface of the metapterygoid. The dorsal margin of the metapterygoid projects laterally in other chaenopsids but in most it is less prominent (state 0). *Neoclinus* has an especially large metapterygoid flap (state 2), a hypothesized apomorphy of that genus (Hastings and Springer, 1994).

Character 7. In all species above node D, the suborbital margin above the upper jaw is bordered by only the first infraorbital (IO1; state 1); IO1 is elongate and IO2 lies dorsal to it. This condition is also seen in *Neoclinus, Mccoskerichthys*, and some species of *Stathmonotus*. In most chaenopsins, IO1 is shorter, IO2 joins it just above the jaw, and the suborbital margin is bordered by both IO1 and IO2 (state 0). Exceptions include *Tanyemblemaria alleni* (Hastings, 1992a) and some species of *Acanthemblemaria* (Hastings, 1990) which exhibit state 1.

Character 8. In all species above node D, the posterior medial margin of the pelvis bears threadlike anterior processes (sensu Stiassny and Moore, 1992) that project anteriorly (state 1; Fig. 2D). Although this character exhibits considerable homoplasy in chaenopsids, most species lack anterior processes (state 0). Exceptions include a few species of *Acanthemblemaria* which have them, but these species are nested within a recently hypothesized phylogeny and appear to have evolved them independently (Hastings, 1990). *Stathmonotus* lacks anterior processes, but they are present in *Neoclinus* and *Mccoskerichthys*.

Node E. - In the most parsimonious topology, *Protemblemaria bicirris* and *P. punctata* form a monophyletic group. These species share five apparent apomorphies.

Character 9. The interorbit of *P. bicirris* and *P. punctata* bears fleshy ridges (state 1). The fleshy ridges continue posteriorly across the nape in *P. punctata* (Böhlke and Cervigón, 1967), while in *P. bicirris*, they do not extend across the nape. However, in *P. bicirris* ossified ridges lie below the fleshy interorbital ridges and continue posteriorly across the frontals. Muscles from the adductor mandibularis complex insert along the lateral margins of these ossified ridges. The interorbit of other chaenopsids lacks fleshy ridges (state 0).

Character 10. The snout of *P. bicirris* and *P. punctata* has a medial fleshy ridge (state 1). The medial portion of the snout of other chaenopsids is flat and lacks a fleshy projection (state 0), although *C. lucasana* is unique in having a medial row of cirri on the snout (state 2).

Character 11. The supraorbital cirri of chaenopsids, when present, vary greatly in shape (Smith-Vaniz and Palacio, 1974, fig. 8), but may be classified in five categories. These include slender and unbranched (state 0), pinnate, with a relatively wide central portion from which several small branches emanate (state 1), palmate, with a few large basal branches (state 2), thick basally, with numerous slender branches (state 3), and flaplike (state 4). *Protemblemaria bicirris* and *P. punctata* have two pairs of supraorbital cirri (see character 50), both of which are more-or-less pinnate (state 1). In both species, the anterior cirrus is the larger and more heavily branched. The number and size of secondary branches increases with increasing size in both species and the degree of branching is greater in *P. bicirris*. The only other chaenopsids with pinnate supraorbital cirri are a few members of the *Acanthemblemaria* clade (Smith-Vaniz and Palacio, 1974; Hastings, 1990, 1992b), but the cirri of these have a more distinct central shaft and smaller and shorter secondary branches than do the cirri of these two species of *Protemblemaria*. The supraorbital cirri of *C. lucasana* and *Mccoskerichthys* are thick basally with numerous thin basal branches (state 3), while the supraorbital cirri of the species of *Emblemariopsis*, when present, are slender and unbranched (state 0). Five species of *Coralliozetus* also have slender, unbranched supraorbital cirri (state 0), while the sixth, *C. rosenblatti*, has flap-like supraorbital cirri (state 4).

Character 12. In *P. bicirris* and *P. punctata*, the dorsal arm of the scapula lacks a stay abutting the cleithrum (state 1). A thin stay abuts the cleithrum (state 0; Hastings, 1992a, fig. 5c) in all other chaenopsids except for some species of *Emblemaria*, in which it is also absent (Hastings 1992a) and presumed to represent an independent loss.

Character 13. In *P. bicirris* and *P. punctata*, as well as in *Neoclinus* and *Mccoskerichthys*, the suture between the anterior and posterior ceratohyals is complex, with 7 or more total interdigitations on the lateral and medial surfaces (state 0; character 22 and fig. 29d in Hastings and Springer, 1994). In most chaenopsids, including *Stathmonotus*, the junc-

tion between the anterior and posterior ceratohyals is simple, with fewer than 6 total interdigitations (state 1; Hastings and Springer, 1994, fig. 29c). This character thus supports node E as a reversal to a complex suture. A similar reversal is also hypothesized within *Acanthemblemaria* (Hastings, 1990).

Node F. - The six species allocated to the genus *Coralliozetus* by Stephens (1963, 1970) share eleven unequivocal apomorphies that appear in both sexes (characters 14-24), and seven unequivocal apomorphies that appear only in females (characters 25-31). Four additional characters (32-35) have multiple equally parsimonious resolutions, one of which supports the monophyly of this clade.

Character 14. In *Coralliozetus*, the dorsal margin of the upper lip has a small V-shaped notch medially (state 1; Hastings, 1995, fig. 7). The dorsal margin of the upper lip of other chaenopsids is continuous and lacks a central notch (state 0), with the exception of *Stathmonotus* which has a deep notch in the upper lip (state 2; character 36 in Hastings and Springer, 1994).

Character 15. In *Coralliozetus*, the fleshy margin of the lower jaw near the mandibular symphysis is notched, forming a fleshy, medial pad (state 1; Hastings, 1995, fig. 7). In other chaenopsids, the fleshy margin along the lower jaw is uninterrupted across the symphyseal region (state 0).

Character 16. In most chaenopsids, the posteriormost branchiostegal is broader distally than proximally (Hastings and Springer, 1994). In *Coralliozetus*, the branchiostegal anterior of the posteriormost is also expanded and bladelike along its distal portion (state 1), while it is thin and little if any wider distally than proximally in other chaenopsids (state 0).

Character 17. Most chaenopsids have a prominent spur on the lateral surface of the hyomandibula (state 1; character 16 in Hastings and Springer, 1994). This spur is absent (state 0) in *Neoclinus*, the sister group of all other chaenopsids (Fig. 1), and in the six species of *Coralliozetus*. Its absence in *Coralliozetus* is inferred to represent a loss of the spur.

Character 18. In all chaenopsids, a process on the dorsal margin of the anteriormost proximal radial (= fused proximal and middle radials, Springer, 1993) of the dorsal fin passes through a hole in the base of the first spine and fuses with the anterior margin of the radial. This radial is "closed" in that it forms a ring joint with the first spine. In *Coralliozetus*, the first and all other proximal dorsal-fin radials supporting spines are "closed" forming ring joints with their associated spines (state 1; Fig. 2E). In other chaenopsids, all proximal dorsal-fin radials posterior to the first are "open" in that the process from the radial passes through a hole in the spine but does not fuse with the anterior margin of the radial (state 0; Hastings and Springer, 1994, fig. 27d). Although some members of the Blenniidae have similar closed proximal radials throughout the spinous dorsal fin (Springer, 1968), within the Chaenopsidae this condition is restricted to *Coralliozetus*.

Character 19. In the anal fin of *Coralliozetus*, most of the proximal radials (= fused proximal and middle radials, Springer, 1993) posterior to the first caudal vertebra are associated with (i.e., lie close to) the posterior margin of a hemal spine. However, in the posterior region of the anal fin, the radials gradually shift posteriorly to become associated with the anterior margin of a hemal spine (state 1; Fig. 2B). In other chaenopsids, all proximal anal-fin radials posterior to the first caudal vertebra are associated with the posterior margin of a hemal spine (state 0; Fig. 2A).

Character 20. In *Coralliozetus*, the ventral portion of the scapula is compressed and higher than it is wide (state 1). In other chaenopsids, the scapula is broad ventrally with a slender dorsal arm (state 0).

Character 21. In *Coralliozetus*, the pelvic spine is small, being reduced to only the proximal portion near its insertion on the pelvis; the distal portion paralleling the first ray is absent (state 1; Fig. 2D). Although small in other chaenopsids, a fully developed pelvic spine is present; the pelvic spine bears both an expanded proximal portion and a distal portion paralleling the first ray (state 0).

Character 22. In *Coralliozetus*, the length and width of the pelvis are similar (state 1; Fig.2D). In other chaenopsids, the pelvis is much longer than it is wide (state 0; Hastings, 1990, fig. 3c).

Character 23. In *Coralliozetus*, the palatine is short, bearing a row of usually six or fewer teeth (state 1; Fig. 2C). In *C. angelicus*, a second more medial row may be present in larger individuals (Hastings, 1991). In other chaenopsids, the palatine is longer, bearing a row of at least six and usually seven or more teeth (state 0; Stephens, 1970, table 2; Hastings, 1992a, fig. 5e; Hastings and Springer, 1994, fig. 22b, 22c), although palatine teeth are absent in *Stathmonotus* (Hastings and Springer, 1994).

Character 24. The upper pharyngeal tooth-bearing bone (infrapharyngobranchial 3) of chaenopsids typically bears a rod-shaped process with a cartilaginous tip (state 0; Fig. 3A). In the species of *Coralliozetus*, this process and its associated cartilage are reduced (state 1; Fig. 3B) or absent (state 2; Fig. 3C). This character was linearly ordered because state 1 is intermediate between states 0 and 2.

Character 25. In female *Coralliozetus*, the lips are rounded and project anteriorly (state 1; Stephens, 1963). In females of other chaenopsids, the lips are flat and do not project anteriorly (state 0). (Males of *Coralliozetus* have flat lips, or state 0).

Character 26. In females of *Coralliozetus*, the posterior anal-fin membrane attaches to the caudal peduncle anterior to the procurrent rays (state 1). In females of most other chaenopsids, the membrane posterior to the last anal-fin element attaches at the base of the caudal fin (state 0). The posterior anal-fin membrane attaches to the caudal peduncle in *Neoclinus* and some members of *the Chaenopsis* clade. (See character 36 for the condition of the anal-fin membrane in males of *Coralliozetus*).

Character 27. In females of *Coralliozetus*, the first dorsal-fin spine lacks a fleshy flap along its anterior margin (state 1; Hastings, 1991). A fleshy flap is present (state 0) along the anterior margin of the first dorsal-fin spine in females of many other chaenopsids and presence of this flap is inferred to be the plesiomorphic for females of the Chaenopsinae (node 4, Fig. 1), although this flap is absent in outgroups of this node. This dorsal-fin flap has been lost in females (as well as males) within *Acanthemblemaria* (Hastings, 1990), within the *Chaenopsis* clade (Hastings, 1992a), and within *Emblemariopsis*. (Males of *Coralliozetus* have a flap anterior to the first dorsal-fin spine, or state 0).

Character 28. In females of *Coralliozetus*, the dorsal fin has a distinct notch between the spinous portion and the segmented-ray portion (state 1), the consequence of a relatively short last dorsal-fin spine (Hastings, 1991). The dorsal fin of females of other chaenopsids has a more shallow or no notch (state 0). (Males of *Coralliozetus* have a shallow dorsal-fin notch, or state 0).

Character 29. The length of the supraorbital cirri of female *Coralliozetus* is less than half of the orbital diameter (state 1). The length of the supraorbital cirri of females of many other chaenopsids (when present) is more than half of the orbital diameter (state 0), although short

cirri are known in females of some species of *Emblemariopsis* (Stephens, 1963, 1970), some members of the *Chaenopsis* clade (Hastings, 1992a), and in *Stathmonotus*. (Males of *Coralliozetus*, except *C. rosenblatti*, have long supraorbital cirri, or state 0).

Character 30. Adults of the relatively plesiomorphic chaenopsids *Neoclinus*, *Mccoskerichthys*, and *Stathmonotus* have four infraorbitals (state 0; character 26 in Hastings and Springer, 1994). Adults of most chaenopsins (node 4, Fig. 1) have two infraorbitals (state 1). The large second infraorbital of chaenopsins represents the fusion of at least two infraorbitals; two separate elements are present in newly settled juveniles but these fuse into the "second infraorbital" during early development (Hastings and Springer, 1994). In females of five of the six species of *Coralliozetus*, these elements do not fuse and three infraorbitals are retained in adults (state 2; Hastings, 1991, fig. 3b). The only exception is *C. cardonae* in which the suture separating IO2 and IO3 is not evident in large females. (Adult males of *Coralliozetus* have two infraorbitals, or state 1).

Character 31. In the relatively plesiomorphic chaenopsids *Neoclinus* and *Mccoskerichthys*, muscles of the adductor mandibularis complex are restricted to the cheek (state 0; character 17 in Hastings and Springer, 1994). In *Stathmonotus* and most of the Chaenopsinae, these muscles cross the temporal sensory canal and insert dorsally on the neurocranium (state 1). In female *Coralliozetus*, these muscles do not cross the temporal sensory canal, but are restricted to the cheek area (state 0). These muscles also do not cover the neurocranium (state 0) in females of *C. lucasana* and some species of *Emblemaria*, and in both sexes of *Lucayablennius zingaro* (Hastings, 1992a). (Males of *Coralliozetus* have these muscles inserted dorsally on the neurocranium, or state 1).

Character 32. In female *Coralliozetus*, the infraorbitals are relatively thin (state 1; Hastings, 1991, fig. 3b), while in females of most other chaenopsids, the infraorbitals are thicker and more heavily ossified (state 0). However, the infraorbitals may be relatively thin in females of several other chaenopsids including *C. lucasana*, and some species *Emblemariopsis, Emblemaria, Chaenopsis* and *Stathmonotus*. Only one of five equally parsimonious reconstructions of this character supports the phylogenetic hypothesis presented in Figure 1. (Males of *Coralliozetus* have relatively thick infraorbitals, or state 0).

Character 33. In females of *Coralliozetus*, the pectoral fins are distinctly pointed, with the central rays being much the longer (state 1). The pectoral fins of females of most other chaenopsids are rounded (state 0). However, the pectoral fins are also pointed (state 1) in females of *C. lucasana* and most species of *Emblemariopsis*. There are two equally parsimonious resolutions of this character on the most parsimonious topology (Fig. 1). In the first, the pectoral of females became pointed at the base of *Coralliozetus* (node F) and at node C (Fig. 1), while in the second, the pectoral fins became pointed at node B and reversed to rounded at node E (Fig. 1). (Males of *Coralliozetus* have rounded pectoral fins, or state 0).

Character 34. The anterofrontal (AFO) sensory pores comprise a bilateral pair of pores between the nasals and the anterior margin of the frontals, and a second, more posterior pair along the interorbit anterior to the commissural pore. Although the anterior pair is present in all chaenopsids, the posterior pair may be present (state 0) or absent (state 1). The posterior pair is absent in all species of *Coralliozetus, P. bicirris*, some members of the *Chaenopsis* clade, and *Stathmonotus* (Hastings and Springer, 1994), but present in *Neoclinus, Mccoskerichthys, Emblemariopsis, C. lucasana, P. punctata*, the *Acanthemblemaria* clade, and some members of the *Chaenopsis* clade. Equally parsimonious resolutions of this character within the *Coralliozetus* clade include loss of the

posterior pair in *P. bicirris* and at the base of *Coralliozetus* (node F), or loss of the pair at node D and reappearance of the pores in *P. punctata*.

Character 35. In *Coralliozetus, Emblemariopsis*, and *C. lucasana*, the mesopterygoid is absent (state 1; Fig. 2C). In other chaenopsids, the mesopterygoid is present (state 0), although in chaenopsins (node 4, Fig. 1), it is reduced in size and restricted to an oval-shaped bone dorsal to the quadrate (Hastings and Springer, 1994, fig. 28b). This character has the same two equally parsimonious resolutions as does character 33; the mesopterygoid was lost independently at nodes C and F, or lost at node B and regained at node E.

Node G. - Within *Coralliozetus, C. angelicus, C. cardonae* and *C. springeri* are hypothesized to form a monophyletic group based on two synapomorphies.

Character 36. In males of these three species, the membrane posterior to the last anal-fin ray is reduced in that it attaches directly to the caudal peduncle (state 1). In males of most other chaenopsids, this membrane is larger and attaches more posteriorly at the caudal-fin base (state 0). However, the posterior anal-fin membrane attaches to the caudal peduncle (state 1) in some members of the *Chaenopsis* clade and in *Neoclinus*. (see character 26 for the condition of the anal-fin membrane in females).

Character 37. These three species of *Coralliozetus* have a relatively short, robust body (state 1), while other chaenopsids are more elongate (state 0). This compact body shape may be related to the microhabitat of these three species. All are known to inhabit vacant barnacle tests, often in areas of strong surge (Hastings, 1986 and personal observations; Acero, 1987).

Node H. - *Coralliozetus springeri* and *C. cardonae* are hypothesized to be sister species based on three apparent synapomorphies.

Character 38. In these two species, the distal portion of the first pleural rib is expanded (state 1). In other chaenopsids, the first pleural rib is slender like the more posterior pleural ribs (state 0).

Character 39. In these two species, the vomerine teeth are distributed in a straight row perpendicular to the long axis of the body (state 1). The vomerine teeth of most other chaenopsids, when present, are arranged in a crescentic row (state 0). Although a straight vomerine tooth row is seen in some species of *Acanthemblemaria*, the crescentic condition is apparently plesiomorphic for that clade (Hastings, 1990).

Character 40. In females of these two species of *Coralliozetus*, the anterior dorsal-fin spines are slightly longer than more posterior spines, resulting in the anterior portion of the dorsal fin being slightly elevated (state 1). Although the shape of the dorsal fin exhibits considerable variation within the Chaenopsidae, the only other species in which the dorsal fin of females is similarly elevated is *P. punctata* (Böhlke and Cervigón, 1967, fig. 1). In most other chaenopsids, the anterior dorsal fin of females is low and even (state 0). The anteriormost three dorsal-fin spines of both sexes of *C. rosenblatti* are elongate (Stephens, 1963), resulting in a spike-like dorsal fin (state 2). (The anterior dorsal fin of males of these two species of *Coralliozetus* is uniformly elevated anteriorly).

Node I. - The remaining three species of *Coralliozetus, C. rosenblatti, C. boehlkei* and *C. micropes*, are hypothesized to form a monophyletic group based on four synapomorphies. Three of these concern morphological details of the pharyngeal jaws.

Character 41. In these species, the ventral flange of ceratobranchial 5, the ventral tooth-bearing bone of the pharyngeal series (Rosen and Patterson, 1990; Williams, 1990), extends relatively far ventrally and forms an acute angle as it extends
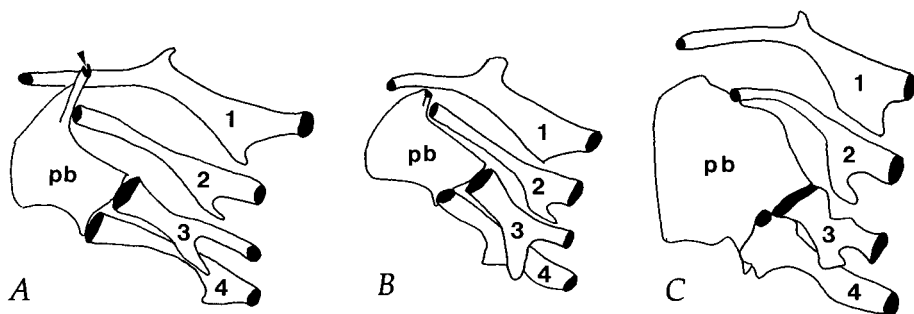
Figure 3. Dorsal view of right upper pharyngeals (infrapharyngobranchial 3, pb, and epibranchials 1-4) of A) *Protemblemaria bicirris* (UAZ 95-3-1), B) *Coralliozetus angelicus* (UAZ 77-42-1), and C) *Coralliozetus micropes* (UAZ 84-17-1). Cartilage is in black. Arrow in A) indicates the cartilage at the tip of the process on infrapharyngobranchial 3 (character 24, state 0). Note that the cartilage and process are reduced (24, 1) in B) and absent (24, 2) in C). Note also the more rounded shape of infrapharyngobranchial 3 (43, 1) in C) compared to the more oval shape (43, 0) in A) and B), the relatively large size of the tip of epibranchial 4 (as large or larger than that of epibranchial 3; 47, 1) in C) compared to that of A) and B) (smaller than epibranchial 3; 47, 0), and the tip of epibranchial 2 that lies above infrapharyngobranchial 3 (48, 1) in C), but lateral to it (48, 0) in A) and B).

dorsoposteriorly (state 1). In other chaenopsids, the anterior margin of the ventral flange does not extend as far ventrally and does not form as acute an angle as it extends dorsoposteriorly (state 0).

Character 42. In these species of *Coralliozetus*, the posterior flange of ceratobranchial 5 is broad and abruptly curves dorsally (state 1; Fig. 2G). In other chaenopsids, the posterior flange is more narrow and curves dorsally more gradually (state 0; Fig. 2F).

Character 43. In these species of *Coralliozetus*, infrapharyngobranchial 3, the dorsal tooth-bearing bone of the pharyngeal series (Springer, 1993), is more-or-less round in dorsal view (state 1; Fig. 3C). In other chaenopsids, infrapharyngobranchial 3 is more oval in dorsal view (state 0; Figs. 3A, 3B).

Character 44. In these species of *Coralliozetus*, the dentary symphysis is broad and the left and right dentaries of adults may be sutured to one another (state 1). In other chaenopsids, the dentary symphysis is relatively narrow and the left and right sides are not sutured (state 0).

Node J. - *Coralliozetus boehlkei* and *C. micropes* are hypothesized to be sister species based on five synapomorphies.

Character 24 (state 2; see above). In these two species, the rod-shaped process on the upper pharyngeal and its associated cartilage are absent (state 2; Fig. 3C). This process and its associated cartilage are reduced (state 1, Fig. 3B) in the other species of *Coralliozetus*, but well developed (state 0; Fig. 3A) in other chaenopsids (Springer, 1993, fig. 1; Williams, 1990, fig. 6; Rosen and Patterson, 1990, fig. 38b).

Character 45. In these two species of *Coralliozetus*, the ventral flange of ceratobranchial 5 is interrupted; the posterior portion of the flange originates medial to the anterior portion of the flange (state 1; Fig. 2G). In other chaenopsids, the ventral flange is uninterrupted across the entire length of ceratobranchial 5 (state 0; Fig. 2F).

Character 46. In these two species of *Coralliozetus*, the ventroposterior margin of the posterior flange of ceratobranchial 5 is thickened (state 1; Fig. 2G). In other chaenopsids, this flange is relatively thin (state 0; Fig. 2F).

Character 47. In these two species of *Coralliozetus*, the end of epibranchial 4 contacting infrapharyngobranchial 3 is as large as, or larger than, the end of epibranchial 3 contacting infrapharyngobranchial 3 (state 1; Fig. 3C). In other chaenopsids, the end of epibranchial 4 contacting infrapharyngobranchial 3 is smaller than the end of epibranchial 3 contacting infrapharyngobranchial 3 (state 0; Figs. 3A, 3B).

Character 48. In these two species of *Coralliozetus*, one end of epibranchial 2 extends to, and lies dorsal to infrapharyngobranchial 3 (state 1; Fig. 3C). In other chaenopsids, this end of epibranchial 2 lies lateral to infrapharyngobranchial 3 near the rod-shaped process (state 0; Figs. 3A, 3B).

HOMOPLASTIC CHARACTERS AND ALTERNATIVE TOPOLOGIES

Character 49. The nasal cirri of three species previously allocated to *Protemblemaria* are branched (state 1), while the nasal cirri of most chaenopsids are unbranched (state 0). Exceptions include *Neoclinus* and some members of the *Acanthemblemaria* clade which have branched nasal cirri (Hastings, 1990). Although this character supports the monophyly of *P. bicirris, P. punctata*, and *C. lucasana* (= *Protemblemaria* sensu Stephens, 1963, 1970), topologies depicting this relationship are four or more steps longer than the most parsimonious.

Character 50. Most species of chaenopsids have a single pair of supraorbital cirri (state 0). The three species previously allocated to *Protemblemaria*, together with *Coralliozetus cardonae* and *C. springeri*, are unique among chaenopsids in having two pairs of supraorbital cirri (state 1; Stephens, 1963; Stephens, Hobson and Johnson, 1966). Other chaenopsids lack supraorbital cirri (state 2; e.g., *Chaenopsis* and allied genera, and some species of *Emblemariopsis*), or typically have more than two pairs of supraorbital cirri (state 3; *Mccoskerichthys* and *Neoclinus*). (*Neoclinus blanchardi* has from one to five pairs of supraorbital cirri; Hubbs, 1953). This character suggests a sister-group relationship between *C. lucasana* and node D (Fig. 1), a topology that is only one step longer than the most parsimonious.

Character 51. The three species previously allocated to *Protemblemaria*, as well as the six species of *Coralliozetus*, lack a second basibranchial (i.e., it is not ossified and not cartilaginous; state 1). The second basibranchial is also absent in some species of *Chaenopsis* (Hastings, 1992a) and in *Stathmonotus* (character 44 in Hastings and Springer, 1994), while it is present (i.e., ossified; state 0) in most chaenopsids. Like character 50, this character supports the sister-group relationship of *C. lucasana* with node D (Fig. 1).

Character 52. The relatively plesiomorphic chaenopsids *Neoclinus, Mccoskerichthys*, and *Stathmonotus* have fewer than three dorsal-fin pterygiophores inserted anterior to the first vertebra (state 0). *Protemblemaria bicirris, C. lucasana,* and some members of the *Chaenopsis* clade are the only chaenopsins (node 4, Fig. 1) with two dorsal-fin pterygiophores anterior to the first vertebra (state 0). Other chaenopsins have three dorsal-fin pterygiophores inserted anterior to the first vertebra (state 1). Although this character supports the sister-group relationship of *C. lucasana* and *P. bicirris*, topologies depicting this relationship are nine or more steps longer than the most parsimonious.

Character 53. In four of the six species of *Coralliozetus*, hypural 5 is absent (state 1), while it is present (state 0) in the other two, plus both species *of Protemblemaria, C. lucasana*, and *Emblemariopsis*. This character exhibits considerable homoplasy in other chaenopsids (Hastings, 1990, 1992a). It supports the most parsimonious topology (Fig.

1) only as a loss of hypural 5 at node F (= *Coralliozetus*) with independent reappearances in *C. springeri* and *C. boehlkei*.

<div align="center">DISCUSSION</div>

This study presents morphological evidence that three nominal genera of chaenopsids, *Coralliozetus, Protemblemaria*, and *Emblemariopsis*, comprise a monophyletic group (node B, Fig. 1), termed the "*Coralliozetus* clade" by Hastings and Springer (1994). Acero (1984a, 1987) also recognized the same clade based on two characters not used in this study, small body size and sexual dimorphism in the color of the head. Small size, SL not over 50 mm and sometimes less than 40 mm (Acero, 1984a, 1987), is characteristic of this clade, but is also widely distributed among other chaenopsids such as some species of *Stathmonotus* (pers. observ.), *Lucayablennius*, the "short-bodied species group" of *Chaenopsis* (Acero, 1984a), the "*caldwelli* species group" of *Emblemaria* (Johnson and Greenfield, 1976), *Emblemaria piratica* (Stephens, 1963), *Ekemblemaria nigra* (Acero, 1984b), and several species of *Acanthemblemaria*, including *A. hancocki, A. greenfieldi, A. medusa, A. aspera, A. spinosa* (Stephens, 1963; Smith-Vaniz and Palacio, 1974), and the miniature *A. paula* (Johnson and Brothers, 1990). Species not exceeding 40 mm SL are thus known from all currently recognized chaenopsid genera except *Neoclinus*, and the monotypic genera *Mccoskerichthys, Hemiemblemaria*, and *Tanyemblemaria* (Hastings, 1992a). Consequently, small body size does not appear to be a reliable indicator of phylogenetic relationships among chaenopsid genera.

The second synapomorphy reported by Acero (1984a, 1987), sexual dimorphism in head coloration, is also not restricted to these genera, but is common among the species of *Emblemaria* (Stephens, 1963; Johnson and Greenfield, 1976; Hastings, 1991) and *Acanthemblemaria* (Stephens, et al., 1966; Smith-Vaniz and Palacio, 1974; Hastings, 1988; Rosenblatt and McCosker, 1988). Consequently, sexual dimorphism in head coloration, like body size, does not appear to be a reliable indicator of phylogenetic relationships among chaenopsid genera.

The *Coralliozetus* clade, together with the *Acanthemblemaria* clade (Hastings, 1990, 1992b) and the *Chaenopsis* clade (Hastings, 1992a), comprise a monophyletic Chaenopsinae (Hastings and Springer, 1994). Stephens (1963, 1970) considered *Protemblemaria* to be the most primitive chaenopsid taxa based on a compilation of several presumed primitive and advanced character states. Consequently he placed this genus at the base of a phylogeny of the Chaenopsidae (= Chaenopsinae, node 4 of Fig. 1). Acero (1984a) came to a similar conclusion (placing *Protemblemaria* sensu lato, *Coralliozetus* sensu stricto, and *Emblemariopsis* as the sister group of the remaining chaenopsins), but did not discuss characters uniting the remaining genera. The present study and Hastings and Springer (1994) hypothesize that the *Acanthemblemaria* clade is the sister group of the other two clades of chaenopsins. However, because this hypothesis is supported by only a single synapomorphy (character 1), further character evidence bearing on the question of relationships among these three apparently monophyletic clades of chaenopsins is desirable. Nonetheless, the hypothesized relationships within the *Coralliozetus* clade (Fig. 1, node B) are robust with respect to its relationships with the other two lineages of chaenopsins.

This study does not support the monophyly of *Protemblemaria* (sensu Stephens, 1963, 1970). This genus originally included two species, *Emblemaria bicirris* Hildebrand, 1946, and *Protemblemaria lucasana* Stephens, 1963, and was diagnosed as having two pairs of supraorbital cirri (Stephens, 1963). A third species, *P. punctata*, subsequently allocated to the genus (Cervigón, 1966; Böhlke and Cervigón, 1967), also has two pairs of supraorbital cirri. However, two species of *Coralliozetus* (see character 50) have two pairs of supraorbital cirri and this character does not unequivocally support the monophyly of *Protemblemaria*. The only character found in this study that supports the monophyly of *Protemblemaria* as delimited by Stephens (1963, 1970), the presence of branched nasal cirri (character 49), is variable in other chaenopsids such as *Acanthemblemaria* (Hastings, 1990). Other character evidence from the present study supports the hypothesis that *P. bicirris* and *P. punctata* comprise a monophyletic group whose sister group is *Coralliozetus*. *Cirriemblemaria lucasana* is the sister group of *Emblemariopsis* (Fig. 1, node C), or the sister group of the two species of *Protemblemaria* plus *Coralliozetus* (see characters 50 and 51). The nomenclatural implications of these hypotheses are discussed below.

The present study strongly supports the monophyly of the genus *Coralliozetus* sensu stricto. These six species share the derived condition of more than 20 characters, several of which (characters 25-31) involve unique character states present only in females.

Relationships of the species of *Coralliozetus* hypothesized here are similar to previous hypotheses with one exception. Stephens (1963) hypothesized *C. boehlkei* to be the sister species of *C. rosenblatti*, while the present study hypothesizes it to be the sister species of *C. micropes*. Topologies placing *C. boehlkei* and *C. rosenblatti* as sister species are five steps longer than the most parsimonious. The hypothesis of Stephens (1963) was apparently based the overall similarity of *C. boehlkei* and *C. rosenblatti*, and did not account for the considerable number of autapomorphies of *C. micropes* (pers. observ.).

NOMENCLATURE ISSUES. —The recent synonymy (Acero, 1984a, 1987) of *Emblemariopsis* Longley, 1927 and *Protemblemaria* Stephens, 1963 with *Coralliozetus* Evermann and Marsh, 1899 bears scrutiny because it has been accepted by the American Fisheries Society's Committee on Names of Fishes (Robins, et al., 1991), has found its way into the literature (Robins and Ray, 1986; Nelson, 1994), and a new species allocated to "*Coralliozetus*" has recently been described (Acero, 1987). Acero based this synonymy on two characters discussed above (body size and color of males), and the assertion that the morphology of the new species *Coralliozetus tayrona* "is a linkage between *Coralliozetus* and *Emblemariopsis* (sensu Stephens, 1970)" (Acero, 1987, p. 18). However, the present study indicates that *C. tayrona* is not intermediate between *Coralliozetus* and *Emblemariopsis*, but is allied with the latter genus in having a truncate neural spine on the penultimate vertebra, a hypothesized synapomorphy of *Emblemariopsis* (see above). Further, *C. tayrona* lacks the twenty two hypothesized synapomorphies of *Coralliozetus* sensu stricto.

Other nomenclatural changes within the *Coralliozetus* clade are warranted because the monophyly of *Protemblemaria* (sensu Stephens, 1963, 1970) is not supported. One solution consistent with the phylogenetic hypothesis (Fig. 1) is to synonymize *Protemblemaria* and *Emblemariopsis* with *Coralliozetus* as done by Acero (1984a, 1987). The effect of this is to designate the "*Coralliozetus* clade" of Hastings and Springer (1994) as the genus *Coralliozetus*. However, this does not recognize the distinctiveness of *Coralliozetus* sensu stricto, and otherwise obscures the phylogenetic relationships of these fishes. A second solution would be to include *Protemblemaria lucasana* Stephens, 1963 in

Emblemariopsis. This is ill-advised because these taxa differ in many respects, *Emblemariopsis* has not been well studied and is in need of revision, and a topology only one step longer than the most parsimonious does not support the sister-group relationship of these taxa.

Consequently, the following nomenclatural actions are proposed. *Coralliozetus* is restricted to the six species above node F (Fig. 1): *Coralliozetus cardonae* Evermann and Marsh, 1900, *Emblemaria micropes* Beebe and Tee-Van, 1938, *Emblemaria angelica* Böhlke and Mead, 1957 (spelling amended to *C. angelicus* to agree with gender of generic name), *Coralliozetus boehlkei* Stephens, 1963, *Coralliozetus rosenblatti* Stephens, 1963, and *Coralliozetus springeri* Stephens et al., 1966. *Coralliozetus tayrona* Acero, 1987 is allocated to *Emblemariopsis*. *Protemblemaria* is restricted to *Emblemaria bicirris* Hildebrand, 1946 and *Protemblemaria punctata* Cervigón, 1966, and a new generic name is provided for *Protemblemaria lucasana* Stephens, 1963.

Cirriemblemaria new genus
Type species: *Protemblemaria lucasana* Stephens, 1963

Diagnosis. —A chaenopsin blenny (sensu Hastings and Springer, 1994), unique in having two rows of cirri extending from the orbit posteriorly across the nape (cirri larger in males than in females), two pairs of deeply branched supraorbital cirri, and males with a single median cirrus on the snout just dorsal to the upper lip. Other distinctive features include exposed nasal ridges, a notch in the supraorbital margin (also in *Mccoskerichthys*), and strong sexual dimorphism (also in *Coralliozetus* and many species of *Emblemaria*).

Etymology. —*cirrus*, L. for tendril, + *emblemaria*, a genus of chaenopsid blennies, in reference to the unique double row of cirri extending across the nape. Gender feminine.

Biogeography. —Two trans-isthmian species pairs (*P. bicirris/P. punctata* and *C. springeri/C. cardonae*) are included in the *Coralliozetus* clade. However, the distributions of members of these pairs differ. *Protemblemaria bicirris* is widespread in the eastern Pacific (Stephens, 1963), while its sister species, *P. punctata*, is restricted to coastal Venezuela (Böhlke and Cervigón, 1967). *Coralliozetus springeri* is found along the Pacific coast of Central America southward to Ecuador (Stephens, et al., 1966), while its sister species, *C. cardonae*, is widespread in the Caribbean (Stephens, 1963; Böhlke and Chaplin, 1968; Acero 1987). The distributions of the Caribbean members of three other transisthmian species pairs of chaenopsids more closely match that of the *Protemblemaria* species pair in that they are restricted to the southern Caribbean (Smith-Vaniz and Palacio, 1974; Hastings, 1990, 1992b). The distributions of the Pacific members of these other transisthmian species pairs is more variable with one being widespread, one being restricted to central America, and one being restricted to the Galápagos Islands (Smith-Vaniz and Palacio, 1974; Hastings, 1990, 1992b).

The remaining species of *Coralliozetus* occur in the eastern Pacific. *Coralliozetus angelicus* occurs in Mexico from the central Gulf of California southward to Acapulco. *Coralliozetus boehlkei* is found along the Mexico coast from Mazatlán southward to Costa Rica and at Isla del Coco (Stephens, et. al., 1966). *Coralliozetus rosenblatti* and *C. micropes* are endemic to the Gulf of California and the adjacent outer coast of Baja California (Stephens, 1963). These distributions imply that speciation in this genus has been centered in the tropical eastern Pacific, especially in the tectonically active Gulf of Califor-

nia region. The chaenopsid genus *Acanthemblemaria* exhibits a similar pattern of recent diversification in the eastern Pacific, especially in the Gulf of California (Hastings, 1990).

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ADDRESS: *Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, E-mail: hastings@u.arizona.edu.*